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ORIGINAL PAPER

Forest Structure Drives Avian Diversity in Boreal Peatland Forests

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Abstract

Peatland forest ecosystems play a critical ecological, economic, and cultural role by sequestering carbon, supporting biodiversity, the provisioning of conventional and non-conventional wood products, and providing habitat for specialists. Historically, forest management in these systems has used clearcut harvests to maximize pulp production, often resulting in structurally simplified stands vulnerable to climate change. As climate change reshapes boreal systems through warming, altered hydrology, and increased disturbance, identifying structural features that promote resilience is increasingly important. Ecological forestry, which aims to emulate natural disturbance and subsequent forest development, is an alternative approach to support a broader suite of ecosystem processes. To inform this approach, we examined how forest structure, quantified through lidar-derived metrics, varies across peatland forest types and stand ages, and how these structural attributes influence avian communities, with emphasis on peatland associate species. We used field measurements, bird point count surveys, and lidar data across productive black spruce, stagnant black spruce, and tamarack stands in lowland conifer peatlands of northern Minnesota. Results showed that canopy height, canopy cover, heterogeneity, vertical canopy complexity, and overall complexity did not differ among cover types but increased significantly with stand age, reflecting the gradual development of structural complexity over time. Total bird species richness and diversity showed limited associations with forest type, stand age, or structural metrics, likely reflecting the broad distribution of generalist species across stands. In contrast, peatland-associated species exhibited clear positive responses: their richness and diversity increased significantly with stand age and were positively correlated with lidar-derived measures of canopy cover and the overall complexity index. These results underscore the ecological value of older, structurally complex peatland stands in sustaining specialist bird assemblages and highlight the importance of incorporating fine-scale structural metrics into biodiversity assessments and climate-adaptive management planning aimed at sustaining habitat function under increasing climatic variability. Further, our results have application to the development of silvicultural

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approaches that better reflect the natural, complex structural dynamics of these ecosystems. Silvicultural approaches that emulate natural structural development, such as irregular shelterwood with reserves or variable density thinning, may enhance canopy complexity while maintaining forest productivity and habitat for peatland specialist birds.

Keywords Peatland forests · Structural complexity · Lidar · Peatland associate species · Boreal biodiversity

Introduction

Peatlands, which make up about one-third of global wetland resources, are among the most valuable ecosystems on Earth, providing diverse ecosystem services such as climate regulation through carbon sequestration, water purification, and cultural and recreational benefits (Wright et al. 1992; Parish et al. 2008). In addition to their ecological functions, peatlands are critical for biodiversity conservation, offering unique habitats for specialized mosses, plants, and wildlife (Soja et al. 2007; Erwin 2009; Kimmel and Mander 2010). In North America, forested peatlands (commonly referred to as lowland conifer forests) are typically dominated by black spruce (*Picea mariana* (Mill.)), tamarack (*Larix laricina* (DuRoi) K. Koch), and northern white cedar (*Thuja occidentalis* L.). The understory is rich in *Sphagnum* mosses, feathermosses (*Pleurozium* spp.), and other bryophytes and vascular plants that thrive in these unique conditions. These forests cover about 3% of the Earth's land surface, including significant coverage across Canada and parts of the United States in Alaska, and the Great Lakes region (defined as Michigan, Minnesota, and Wisconsin) (Parish et al. 2008; Rydin et al. 2013).

Habitat complexity in peatlands is shaped by features such as canopy layering and understory density that vary spatially, which combine to create a variety of microhabitats that support species with diverse ecological requirements (McElhinny et al. 2005; Kovalenko et al. 2012; Page and Baird 2016; Thompson et al. 2017; Girona et al. 2023). This complexity is especially important in boreal forested peatlands, where many wildlife species are habitat specialists that rely on specific structural conditions for breeding, foraging, and shelter (Imbeau et al. 2001; Hadley and Desrochers 2008; Laaksonen and Lehikoinen 2013). Historically, peatland structural complexity developed under infrequent stand-replacing fires occurring at intervals of approximately 200 to 500 years (Heinselman 1973). Long fire-free periods following regeneration allowed structural heterogeneity to accumulate through recurring minor to moderate severity disturbances, including windthrow, mortality from eastern dwarf mistletoe (*Arceuthobium pusillum*), insect outbreaks (e.g. eastern larch beetle (*Dendroctonus simplex* LeConte)), and hydrologic variability (McKee et al. 2022; Gray et al. 2025). This localized disturbance produced canopy gaps and coarse woody debris at fine to moderate spatial scales, resulting in irregular, multi-cohort stands characterized by gap dynamics within a broad range of variability across the landscape (Heinselman 1973; Cyr et al. 2009). Evidence from northern peatland

plant communities suggests that these finer-scale disturbances likely occurred at intervals of roughly 70–120 years, contributing substantially to structural diversity even in the absence of stand-replacing fire (Aaseng et al. 2011). However, climate change is altering the disturbance processes that historically structured these systems, as projected warming is expected to intensify drought, alter hydrology, and potentially shorten fire return intervals, thereby truncating stand development outside its historic range of variability (Flannigan et al. 2009; Dieleman et al. 2020, IPCC 2021). Maintaining structural heterogeneity through ecological silvicultural practices may therefore be critical for sustaining biodiversity and climate resilience (Dieleman et al. 2015; Kuuluvainen and Gauthier 2018).

In the context of forest management, peatland forest communities have been typically managed using clearcut regeneration harvests during the stem exclusion stage of stand development (Anderson et al. 2020; Skay et al. 2021; but see Windmuller-Campione et al. 2020 for reduced levels of clearcut regeneration harvests in Minnesota, USA), the timing of which varies with site productivity. Clearcutting is thought to emulate stand-replacing fire but that often reduces vertical layering and structural legacies, resulting in more homogeneous stand conditions than those produced by natural disturbance regimes (Thompson et al. 2003; Brassard and Chen 2006; Kuuluvainen and Gauthier 2018; Liu et al. 2024; Raymond et al. 2023; Lunde et al. 2025). For example, studies have documented significant reductions in vertical canopy layering and coarse woody debris following clearcut regeneration harvests, which contribute to homogenized habitat conditions (Raymond et al. 2023; Lunde et al. 2025). Such structural simplification can alter vegetation dynamics and spatial disturbance patterns, fragmenting landscapes in ways that do not fully reflect the patchiness and temporal variability that is characteristic of historical disturbance regimes such as wildfire and windthrow (Wagner 1978; Cyr et al. 2009; Bouchard and Pothier 2011; Boucher et al. 2016; Anyomi et al. 2022).

Loss of habitat complexity is particularly concerning in the North American boreal forest, a globally important breeding ground for billions of birds that also serve as key indicators of biodiversity (Wells and Blancher 2011; Rosenberg et al. 2019). Because birds respond rapidly to habitat changes and reflect broader ecosystem conditions, they are widely recognized as indicators of forest health and environmental change, making forestry practices that account for bird habitat needs an important component of sustainable management (Niemi et al. 1998; Lindenmayer et al. 2000; Venier and Pearce 2004; Fraixedas et al. 2020). Given that, preserving biodiversity and modifying forestry practices to reduce ecological impacts have emerged as central goals in sustainable forest management (Myers et al. 2000; Lindenmayer and Franklin 2013). In response to growing societal concern over biodiversity loss, boreal forest management has increasingly begun to incorporate values beyond timber production using ecological forestry (Dobson et al. 1997; Franklin et al. 2002; Gauthier 2009; Halme et al. 2013; Kuuluvainen 2002; Puettmann et al. 2009). Ecological forestry broadly attempts to utilize silvicultural practices that mimic natural disturbance regimes, with emphasis on retention of structural legacies during intermediate treatments or regeneration harvests. Approaches such as retention harvesting, variable-density thinning, and extended rotation periods aim to balance timber production with ecological integrity by maintaining legacy structures

and promoting diverse successional pathways (Franklin et al. 2002; Puettmann et al. 2009; Kuuluvainen and Gauthier 2018).

Despite the growing consensus on the importance of structural complexity, these attributes remain under-characterized in many peatland systems, particularly in relation to age and composition. Gaining a clearer understanding of how structural attributes vary across forest types and developmental stages is essential for providing quantifiable structural targets to guide sustainable forest management and biodiversity conservation efforts. Quantifying linkages between structural complexity and avian communities will help support the use of ecological forestry. This study explores how habitat complexity varies across forest types and developmental stages in peatland ecosystems, and how these structural differences are related to avian communities. We quantified forest structure using six lidar-derived metrics and developed a composite index to represent overall structural complexity. Specifically, our objectives were to: 1.) quantify variation in forest structure across forest types and age using lidar-derived metrics, 2.) examine patterns of bird species richness, diversity, and community composition to understand how they vary with forest type, age, and structural complexity, and 3.) characterize relationships between peatland-associated bird communities and structural complexity across cover types and developmental stages, including identification of indicator species. By linking structural complexity to avian community responses, this study provides empirical insight into how peatland forest management may be adapted to sustain biodiversity under projected climate-driven disturbance regimes.

We hypothesized that structural complexity would increase with stand age across all forest types, with stands in later developmental stages exhibiting greater canopy heterogeneity and vertical layering. In particular, we expected productive black spruce, and eastern larch stands to exhibit greater canopy heterogeneity earlier in stand development than stagnant black spruce stands. While overall avian richness and diversity were expected to remain relatively consistent, we anticipated shifts in community composition driven by structural differences. Specifically, we predicted that peatland associate species, species with narrow ecological requirements, will be more strongly associated with structurally complex, late-successional stands.

Methods

Study Area

The study area was located in northern Minnesota, USA, within the Laurentian Mixed Forest Province, which includes the Northern Minnesota and Ontario Peatlands and the Northern Minnesota Drift and Lake Plains ecological regions (Griffin 1977, McFarlane et al. 2018; Figure 1). The study area spans two degrees of latitude, from 25 km north of Mille Lacs Lake (46.6°N) to 5 km south of Lake of the Woods (48.9°N). The region has a continental climate with cold, dry winters (January average temperature −15 C) and warm, humid summers (July average air temperature 19 C).

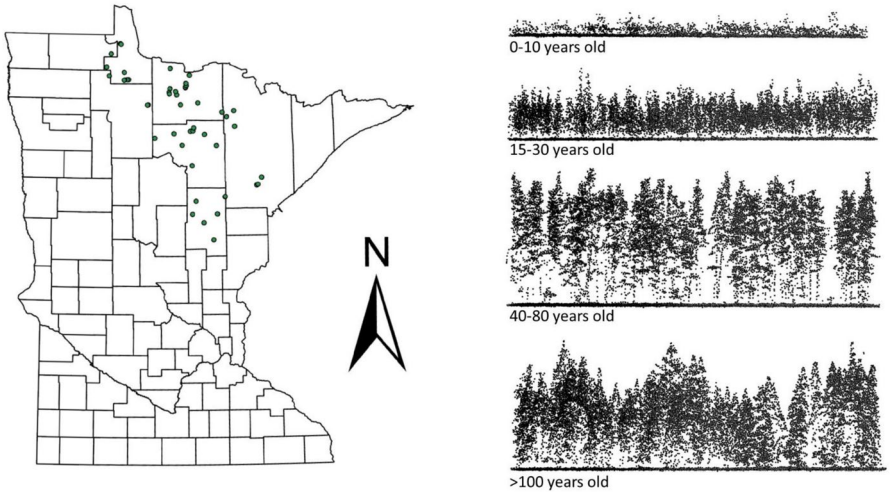

Fig. 1 Map of study sites across northern Minnesota, USA. Each dot represents a site (forest stand) surveyed for this study. Lidar images show progression of forest structure with aging stands. All lidar images are from productive black spruce stands and are shown at the same spatial scale

The study used a chronosequence approach to assess effects of time since disturbance and forest cover type. Three forested peatland types were evaluated: productive black spruce, stagnant black spruce, and tamarack, as defined by the Minnesota Department of Natural Resources Native Plant Community classification (Aaseng et al. 2011). These forest types represent distinct ecological types within forested peatlands and are characterized by differences in species composition, site productivity, and hydrologic conditions. Site index, a measure of site productivity (Viereck and Johnston 1990), was used to differentiate between stagnant and productive black spruce where sites with dominant and co-dominant trees <7m tall at age 50 were classed as stagnant, and those >7m classed as productive. Differences in site productivity between these site types are driven by differences in hydrology and their influence on nutrient availability and growing conditions. For each of these cover types, we used forest inventory records to determine age, and stands were subdivided into four age classes for site selection: <10, 15–30, 40–80, and >100 years since the most recent stand replacing event. In most cases, this disturbance reflected timber harvest within a managed forest matrix, although for some older stands the precise origin (harvest versus natural stand-replacing disturbance) could not be determined with certainty from available records. The overall experimental design is a two-way factorial with four replications per treatment combination (n = 48 for all combinations of 3 cover types x 4 age classes). More detail on the study area and design can be found in Stelling et al. (2023).

Site and Lidar Characteristics

Site characterization of forested peatland stands across northern Minnesota included nine variables: cover type (productive black spruce, stagnant black spruce, and tamarack), stand age, along with six lidar-derived structural metrics and a composite index of overall complexity. Forest stand boundaries were delineated using the Forest Inventory Management dataset and verified with high-resolution satellite imagery and field visits (MN DNR 2016). Stand sizes varied widely, ranging from 26 to 473 acres, with a mean of 99 acres and a median of 66 acres. The study sites within the stands included six vegetation plots (11.3 m radius; 0.04 ha) and two point-count (100 m radius; 3.14 ha) locations arranged in relation to the stand centroid. Point-count stations were placed in a randomly assigned direction from the centroid to maximize their distance from stand boundaries and were spaced at least 250 m apart to minimize overlap. Stand age was refined by collecting increment cores at breast height (1.3 m above ground) from 24 trees per site (four trees per plot across six plots) for all stands except those in the <10-year age class. Cores were mounted, sanded, and tree age was determined by counting annual rings, with an additional five years added to account for the time needed for trees to reach coring height (Carmean et al. 1989). Due to occasional unusable cores, final sample sizes per site ranged from $n = 20$–24. In stands younger than 10 years, trees were either too small or absent for coring; therefore, stand age was assigned based on documented harvest year derived from harvest records and aerial imagery.

Lidar data were obtained from multi-year airborne surveys conducted during the spring seasons of 2021 and 2022 (Table 1). These structural metrics were generated from a multi-year, statewide airborne lidar dataset collected during the spring between April 16 and May 17, 2021, for the Rainy Lake region; April 25 to May 18, 2021, for the Lake Superior region; and May 23 to July 30, 2022, for the Upper Mississippi River region (Table 1; Minnesota Geospatial Information Office [MnGeo], 2021-2025). All flights adhered to USGS Quality Level 1 (QL1) specifications, ensuring consistent acquisition methods across regions, including a nominal pulse density of at least 8 pulses per square meter and vertical accuracy meeting QL1 standards. Lidar data were unavailable for two stands due to USGS data redaction applied to tiles overlapping tribal reservation boundaries; therefore, analyses incorporating lidar-derived variables were conducted on a reduced dataset ($n = 46$). We used FUSION software (McGaughey 2016) to summarize forest structural variables for each surveyed forest stand. To normalize lidar return heights to height above ground level, we employed 0.5-meter resolution digital elevation models representing the bare-earth surface. We then overlaid a 20 m grid across the area surrounding each forest stand and calculated canopy height, canopy cover, canopy heterogeneity, rumple, and understory cover and variation in understory cover. Canopy height metrics were based on the 75th percentile of non-ground return heights. Canopy cover was defined as the proportion of first returns that were ≥1 m above ground (Lefsky et al. 2002). Canopy heterogeneity was calculated as the standard deviation of return height above ground. The understory cover index was calculated as the proportion of non-ground lidar returns occurring below 2 meters (Wing et al. 2012), with values ranging from 0 (no understory) to 1 (dense understory). Lidar metrics were

Table 1 Variables considered for peatland analyses, including forest cover type, stand age, canopy and understory structure, and canopy heterogeneity metrics

Variable	Scale	Description	Data source
Forest cover type	Stand age and structure	Forest type based on Native Plant Community; categories include: productive black spruce (*Picea mariana*), stagnant black spruce, and tamarack (*Larix laricina*)	MN DNR
Stand age	Stand age and structure	Estimated mean age of trees at each study site, measured in years. For most stands, determined by counting growth rings on increment cores collected at breast height (4.5 feet) and adding five years to account for time to reach coring height. For stands < 10 years old, estimated from harvest year based on records and aerial imagery	Tree cores or known harvest date
Canopy height	Stand age and structure	Mean 95th percentile of non-ground return height; calculated by taking the mean of all raster pixels within the stand polygon; represents the average stand height of the entire stand area	Lidar
Canopy cover	Canopy characteristics	Mean canopy cover value for stand, calculated using first returns only (2 m threshold for canopy vs. understory)	Lidar
Understory cover	Understory	Mean understory cover index (2 m threshold for canopy vs. understory)	Lidar
Variation in understory cover	Understory	Standard deviation in understory cover index values (2 m threshold for canopy vs. understory)	Lidar
Canopy heterogeneity	Canopy structure	Mean Standard deviation of return heights	Lidar
Rumple	Canopy structure	A measure of vertical canopy complexity and represents roughness of the canopy surface. It is calculated as the ratio of canopy outer surface area to ground surface area. Higher rumple values indicate a more structurally heterogeneous and complex canopy	Lidar
Overall complexity index	Canopy structure	An integrated metric based on the standardized sum of three lidar-derived variables: canopy cover, canopy heterogeneity, and rumple, representing both horizontal and vertical structural complexity	Lidar

Variables were derived from field sampling and lidar data

calculated using lidar returns from the study sites (i.e. combined survey locations) within each stand and summarized for analysis.

We developed a composite index of overall complexity using three complementary lidar-derived metrics. These included 1.) canopy cover, representing the proportion of area covered by canopy at the first return height threshold, 2.) canopy heterogeneity, capturing horizontal heterogeneity in canopy cover across the stand, and 3.) rumple, a measure of vertical canopy complexity, calculated as the ratio of canopy surface area to ground area. Each of these metrics was standardized on a scale from 0 to 1 to ensure comparability, and the standardized values were summed to produce a single, integrated measure of overall habitat complexity.

Avian Point Count Surveys

Point counts were conducted during the peak breeding season (late May to early July) of 2019 and 2020 by experienced observers who had successfully completed a standardized training, including passing a hearing and identification proficiency test (see Niemi et al. 2016). Following a standardized monitoring protocol (Niemi et al. 2016; Grinde et al. 2025), we conducted two 10-minute, unlimited-distance point-count surveys within each stand and combined detections to generate stand-level bird community metrics. Detections of all species were recorded, noting the distance and time of detection at one-minute intervals throughout the survey period. We also recorded survey covariates (e.g., time of day, wind, sky code) at each point. Trained observers conducted the surveys during the early morning activity period, beginning roughly 30 minutes before sunrise and continuing up to four hours after sunrise. All counts were conducted under favorable weather conditions (e.g., low wind speeds <15 km/hr and minimal or no precipitation). Birds detected beyond a 100-m radius, as well as flyovers, were excluded from all analyses to maintain comparability across stands.

Data Analysis

Lidar To assess patterns in lidar-derived metrics related to stand age and cover type, we used analysis of covariance (ANCoVA). For each lidar variable and the overall complexity index, we fit a full model including main effects and their interaction. Prior to analysis, we examined model assumptions by inspecting residual plots for homoscedasticity, applying Shapiro–Wilk tests for normality, and checking for influential observations using Cook's distance. Rumple was $\log_{10}$-transformed prior to analyses to alleviate heteroscedasticity, whereas other residuals did not have notable departures from normality. We assessed ecological relevance by examining the size and direction of standardized beta coefficients along with their confidence intervals. Predictors were considered statistically significant at $\alpha = 0.05$. When cover type effects were significant, we conducted post-hoc pairwise comparisons using Tukey's adjustment for multiple testing. For constrained variables (e.g., percent canopy cover), which violate normality and boundedness assumptions, we used beta regression (betareg package; Cribari-Neto and Zeileis 2010).

Bird Community Metrics Bird communities were summarized using species richness (number of species per stand) and the Shannon–Wiener diversity index. We also calculated richness and diversity metrics for peatland associated species, defined as species consistently associated with forested peatlands (commonly referred to as lowland conifer forest associates) following criteria from Green (1995), Niemi et al. (2016), and Pfannmuller et al. (2024; Appendix Table 2). In our study area, most of these species function as habitat specialists, occupying distinct ecological niches within forested peatland systems and collectively reflecting key aspects of peatland bird community composition (Appendix Table 2). The identified group ($n = 15$) included Black-backed Woodpecker (*Picoides arcticus*), Blue-headed Vireo (*Vireo solitarius*), Boreal Chickadee (*Poecile hudsonicus*), Canada Jay (*Perisoreus canadensis*), Connecticut Warbler (*Oporornis agilis*), Dark-eyed Junco (*Junco hyemalis*), Golden-crowned Kinglet (*Regulus satrapa*), Lincoln's Sparrow (*Melospiza lincolnii*), Purple Finch (*Haemorhous purpureus*), Ruby-crowned Kinglet (*Regulus calendula*), Olive-sided Flycatcher (*Contopus cooperi*), Palm Warbler (*Setophaga palmarum*), White-winged Crossbill (*Loxia leucoptera*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), and Yellow-rumped Warbler (*Setophaga coronata*). All metrics were calculated separately for each stand and year, then averaged across the two years to account for potential annual variability. To evaluate the effects of stand age and cover type on bird community metrics, we applied the same ANCoVA modeling framework described above. Analyses were conducted for the full bird community and then repeated for the subset of peatland associate species to determine whether these species exhibited distinct patterns relative to forest structure and composition. Finally, we used Principal Components Analysis (PCA, rda function in vegan package; Oksanen et al. 2025) to explore relationships between lidar-derived structural metrics and bird richness and diversity. Lidar-derived metrics were standardized prior to PCA, and the resulting PCA axis scores were used in simple linear regression with bird community metrics.

Community Composition To explore patterns in bird community composition and visualize key ecological gradients, we applied non-metric multidimensional scaling (nMDS) using the metaMDS function in the vegan package (Oksanen et al. 2025) with $k = 3$ and Wisconsin double standardization. Ordination stability was assessed by solution convergence (best solution repeated 12 times), overall stress (0.12) and by plotting multiple iterations ($n = 5$) to ensure solutions are similar. Bird abundance data were averaged across the two survey years, and rare species (occurring at fewer than three sites) were excluded to improve ordination stability and interpretability. Multiple response permutation procedure (MRPP, mrpp function in vegan, with Euclidean distance) with 9999 permutations was used to assess the significance of group separation. To identify bird species strongly associated with gradients in overall structural complexity, we conducted Indicator Species Analysis following Dufrêne and Legendre (1997), implemented via the indicspecies package (De Cáceres and Legendre 2009). We report Indicator Value (IndVal) statistics as a square root of IndVal and p-value based on 999 permutations, with higher IndVal and a significant p-value indicating a stronger association. All statistical analyses were performed in R version 4.5.1 (R Core Team 2025).

Results

Lidar Metrics

Across all stands ($n = 46$), the average canopy height was 7.8 meters, ranging from just over 1 meter to 16 meters. Canopy height increased significantly with stand age (ANCoVA $F_{age} = 60.4$, $p < 0.01$; Figure 2) and was different across cover types (ANCoVA $F_{covertype} = 6.9$, $p < 0.01$); the interaction between age and cover type was not significant ($p = 0.86$; see Table S1 for detailed model outputs). Post-hoc comparisons showed that canopy height was significantly lower in stagnant black spruce compared to tamarack (difference = -3.45 ± 0.93 meters, $p < 0.01$), while differences between productive black spruce and tamarack (difference = -1.87 ± 0.95 meters, $p = 0.13$) and between productive black spruce and stagnant black spruce (difference = 1.58 ± 0.93 meters, $p = 0.22$) were not statistically significant.

Canopy cover exhibited substantial variation, from near-zero to nearly 94% (mean 46%), indicating dense canopies in some stands. Canopy cover also increased significantly with age (beta regression z = 4.8, $p < 0.01$), increasing more than 10-fold from youngest to oldest stands, with a slightly higher cover in tamarack compared to productive and stagnant black spruce (z = 2.3 $p = 0.02$). Canopy heterogeneity (a

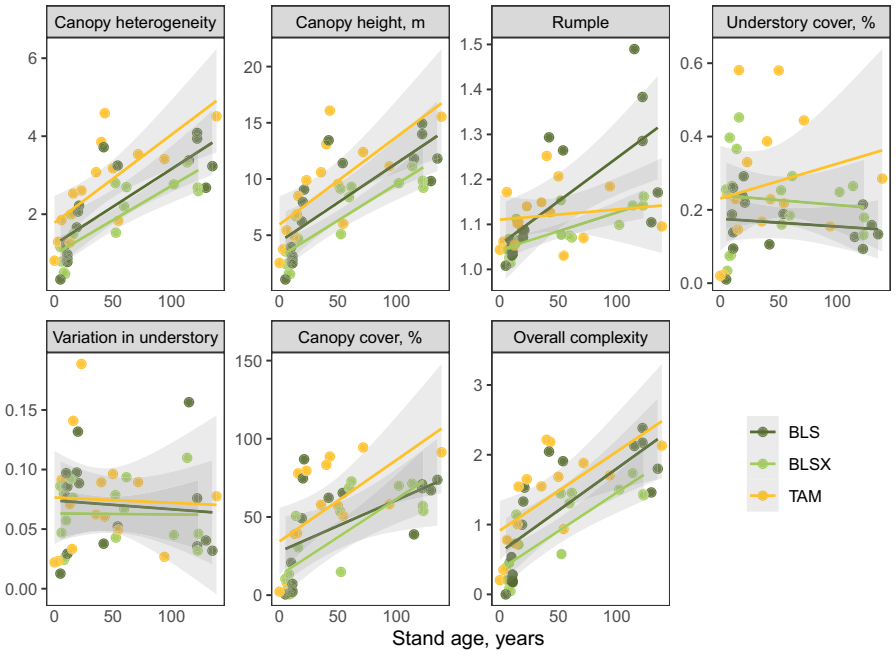

Fig. 2 Variation in lidar-derived forest structure metrics across stand age and cover type. Lidar metrics are grouped by forest cover type (productive black spruce (BLS), stagnant black spruce (BLSX), and tamarack (TAM)) and plotted across a gradient of stand ages. The shaded area is 95% confidence band for the estimated regression line

metric of variability in vertical structure) averaged 2.25 (SD = 1.17). Canopy heterogeneity increased with age (ANCoVA $F_{age} = 60.4$, $p < 0.01$) and varied across cover types ($F_{covertype} = 8.0$, $p < 0.01$; the interaction between age and cover type was not significant $p = 0.75$). Post-hoc comparisons across all ages showed that canopy heterogeneity was significantly lower in productive black spruce compared to tamarack (difference = -0.69 ± 0.26, $p < 0.01$), and in stagnant black spruce compared to tamarack (difference = -1.02 ± 0.26, $p < 0.01$). The contrast between productive black spruce and stagnant black spruce was not statistically significant ($p = 0.39$).

The rumple index (a measure of vertical canopy complexity) averaged 1.12 and ranged from 1.01 to 1.49. The interaction between age and cover type was significant for rumple (ANCoVA interaction between age and cover type $F_{interaction} = 3.8$, $p = 0.03$) and the increase with age (overall age effect ANCoVA $F_{age} = 22.8$, $p < 0.01$; Figure 2) was more pronounced in both types of black spruce (productive black spruce $R^2 = 0.45$, $p < 0.01$, stagnant black spruce $R^2 = 0.60$, $p < 0.01$) and absent in tamarack (simple linear $p = 0.63$). Understory cover varied substantially among stands, ranging from 0.01 to 0.58 (mean = 0.22); ANCoVA results indicated no significance of the main effects or the interaction (ANCoVA age effect $p = 0.82$, cover type $p = 0.10$, interaction effect $p = 0.53$). Similarly, there were no significant relationships between the variation in understory cover and main or interaction effects (ANCoVA age effect $p = 0.71$, cover type $p = 0.71$, interaction effect $p = 0.98$; Figure 2). Overall complexity index ranged from 0 to 2.4, with the theoretical maximum of 3 standardized weights (sum of three standardized components: canopy cover, canopy heterogeneity and rumple). Overall complexity index increased significantly with stand age (ANCoVA $F_{age} = 49.6$, $p < 0.01$; Figure 2), with an approximately 10-fold increase between the youngest and the oldest stands. The effect of cover type was also significant (ANCoVA $F_{covertype} = 5.5$, $p < 0.01$), whereas the interaction between age and cover type was not ($p = 0.96$). Post-hoc comparisons showed that overall complexity index was significantly lower in stagnant black spruce compared to tamarack (difference = -0.58 ± 0.17, $p < 0.01$), while differences between black spruce and tamarack (difference = -0.28 ± 0.17, $p = 0.25$) and between black spruce and stagnant black spruce (difference = 0.30 ± 0.16, $p = 0.20$) were not statistically significant.

Bird Community Metrics

Avian surveys conducted across peatland forest sites recorded a total of 1,037 individual detections representing 63 species (Appendix Table 3). The most frequently observed species were Nashville Warbler (*Vermivora ruficapilla*; $n = 269$), White-throated Sparrow (*Zonotrichia albicollis*; $n = 123$), Common Yellowthroat (*Geothlypis trichas*; $n = 77$), Palm Warbler (*Dendroica palmarum*; $n = 60$), and Lincoln's Sparrow (*Melospiza lincolnii*; $n = 45$). Across all surveyed stands, birds detected averaged 11 individuals per stand (SD = 4.5), species richness averaged 6 species per stand (SD = 1.7), and Shannon–Wiener diversity averaged 1.5 (SD = 0.3).

Total species richness did not vary significantly across stand age and cover types (ANCoVA $F_{age} = 1.3$, $p = 0.29$; $F_{covertype} = 1.0$ $p = 0.31$; $F_{interaction} = 2.0$, $p = 0.15$). Overall, Shannon–Wiener diversity also did not vary significantly across cover types and stand age (ANCoVA all $p > 0.15$ for age, cover type and interaction). Peatland associate species richness showed a significant positive association with stand age (ANCoVA $F_{age} = 6.9$, $p = 0.01$) but not cover type ($p = 0.49$) or the interaction ($p = 0.47$; Figure 3). Similarly, Shannon–Wiener diversity of specialists was also positively associated with stand age (ANCoVA $F_{age} = 4.3$, $p = 0.05$) but not cover type or the interaction effect ($p > 0.65$; Figure 3).

The Principal Component Analysis of age and lidar complexity predictors (including canopy heterogeneity, canopy cover, canopy height, rumple, understory cover density and variation in understory cover density, overall complexity index) identified two primary axes in the reduced dimensional space, explaining 70% and 16% of the overall variation for PC1 and PC2, respectively. Predictors loading the most on the first principal component included, in the order of decreasing importance, overall complexity index, canopy cover, canopy height, canopy heterogeneity and age (Figure 4). For the second principal component, the highest-loading positive predictor included age, and negative-loading predictors included understory cover and variation in understory cover. The PC1, which was summarizing multiple increasing complexity metrics, did not have a significant correlation with overall bird diversity and richness, but had a significant positive correlation with specialist diversity and richness (linear $R^2 = 0.15$,p

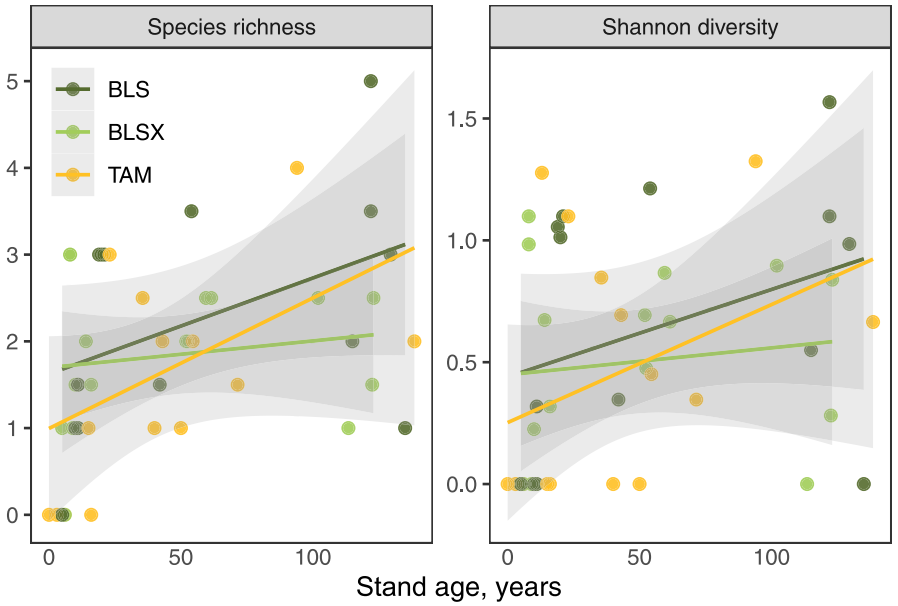

Fig. 3 Relationships between stand age and peatland associate bird community metrics. Plots show relationships between stand age and peatland associate species richness and Shannon–Wiener diversity grouped by forest cover type (productive black spruce (BLS), stagnant black spruce (BLSX), and tamarack (TAM)) and plotted across a gradient of stand ages. The shaded area is 95% confidence band for the estimated regression line

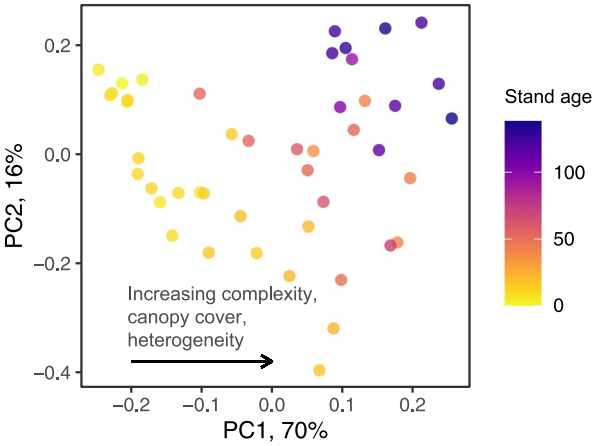

Fig. 4 Biplot of the first two principal components from a PCA of lidar-derived structural metrics. PC1 (70%) represented increasing canopy structural complexity, with strong contributions from overall complexity, canopy cover, canopy height, heterogeneity, and age. PC2 (16%) contrasted age with understory structure

< 0.01 and $R^2 = 0.13$, $p < 0.01$, for peatland associate richness and diversity, respectively; Figure 5; see S1 and S2 for associations with individual lidar metrics).

Community Composition and Indicator Species

Non-metric multidimensional scaling (nMDS) analysis was used to reduce the dimensionality of bird community data and identify major gradients in community composition. The nMDS ordination ($k = 3$, stress = 0.12, rare species cut-off = 3) revealed clear patterns in bird assemblages across peatland forest types. In particular, older black spruce forests were associated with greater abundance of specialist species indicating distinct community composition in these stands (MRPP for cover types $p = 0.02$, Figure 6).

This pattern was further supported by the results of the Indicator Species Analysis, which identified several bird species significantly associated with the overall complexity index. Several peatland specialist species were significantly associated with more complex habitats, including Yellow-rumped Warbler (ISA = 0.77, $p < 0.01$), Golden-crowned Kinglet (ISA = 0.72, $p < 0.01$), and White-winged Crossbill (ISA = 0.47, $p = 0.05$). In contrast, species linked to less complex, more open habitats included two peatland specialists, Lincoln's Sparrow (ISA = 0.76, $p < 0.01$) and Palm Warbler (ISA = 0.75, $p < 0.01$), and three generalist early-successional species American Goldfinch (*Spinus tristis;* ISA = 0.59, $p = 0.02$), Song Sparrow (*Melospiza melodia;* ISA = 0.50, $p = 0.03$), and Savannah Sparrow (*Passerculus sandwichensis;* ISA = 0.47, $p = 0.05$).

Discussion

This study provides insight into how forest structure varies across peatland forest types and developmental stages, and how these attributes relate to avian communities, particularly peatland associate species. By integrating lidar data with bird

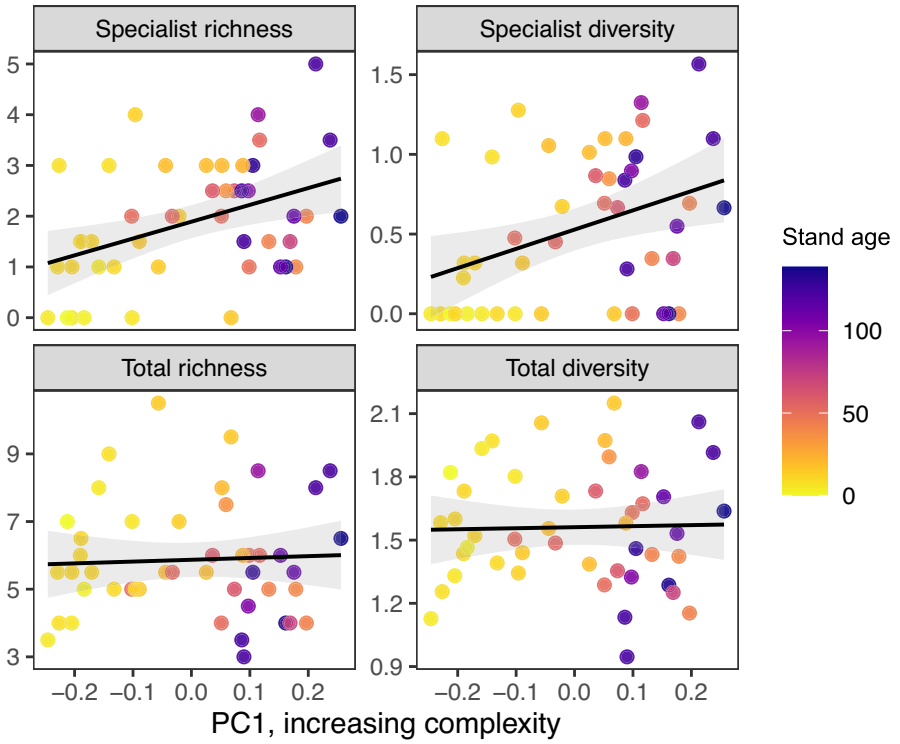

Fig. 5 Correlations between the first principal component (PC1, increasing complexity) and bird community metrics including total richness and diversity (lower panel) and peatland associate species richness and diversity (upper panel)

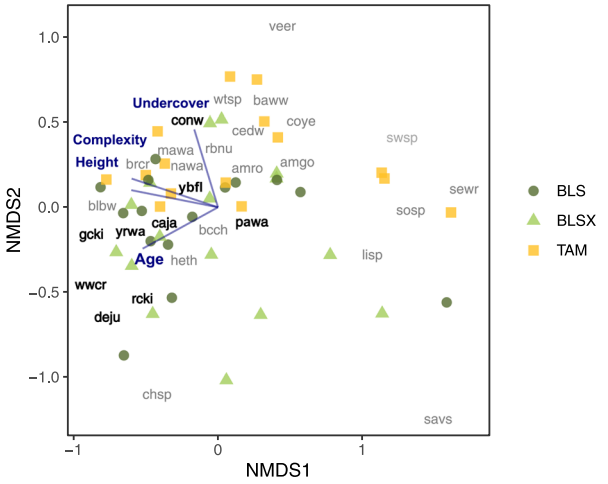

Fig. 6 Non-metric multidimensional scaling (nMDS) ordination of bird community composition across peatland forest types. Environmental vectors representing stand age, canopy height, structural complexity, and understory cover are overlaid to illustrate key habitat gradients. Bird species are labeled using four-letter codes (see Appendix Table 3), and symbols differentiate between peatland associate species and non-specialists

community surveys, we offer one of the first detailed assessments of the interaction of habitat complexity and forest stand age in peatlands of northern Minnesota. We found that canopy height, canopy cover, canopy heterogeneity, rumple, and the overall complexity index increased significantly with stand age, reflecting the gradual development of habitat complexity over time. While overall bird richness and diversity showed no clear relationships with age or cover type, likely due to the broad distribution of generalist species, peatland associate species exhibited a strong positive response to stand age. Peatland associate species richness and diversity increased significantly with stand age and were positively associated with several structural complexity metrics, including canopy cover, height, and heterogeneity. Understory variation showed weaker associations, suggesting that canopy-level complexity is a stronger driver of peatland associate diversity than understory structure. These patterns indicate that older, more structurally complex peatlands support specialized bird communities, whereas younger, less complex stands tend to favor generalist species. Collectively, these findings highlight the ecological importance of mature, structurally complex peatland forests in maintaining specialized avian assemblages and reinforce the value of incorporating fine-scale structural metrics into biodiversity assessments. Understanding how structural attributes vary across forest types and developmental stages is critical for setting structural targets that support ecological forestry and biodiversity conservation. Our findings provide a foundation for refining silvicultural practices to align with ecological forestry and promote structurally complex forests, enhancing habitat quality and resilience under changing environmental conditions.

Patterns in structural variation across peatland stands revealed consistent differences in the relative importance of stand age and cover type as predictors of forest structure. Consistent with our hypotheses, several aspects of structural diversity, including canopy cover, canopy heterogeneity, and the rumple index, increased significantly with stand age. These relationships reflect the gradual development of vertical complexity as stands mature, with older forests exhibiting taller canopies, more vertical layering, and greater surface roughness (Bradford and Kastendick 2010). Age-related changes were especially pronounced in tamarack stands, which showed greater canopy heterogeneity, more developed understory layers, and higher vertical structure compared to stagnant black spruce stands. Tamarack forests are richer and more productive peatland cover types and often support more diverse understory plant communities due to greater light availability beneath their more open canopies (Majasalmi and Rautiainen 2020). This increased productivity and openness promote faster successional development relative to black spruce, and the shorter lifespan of tamarack means that shade-tolerant and longer-lived species can establish and recruit earlier in stand development (Burns and Honkala 1990). These stands can develop structural complexity quickly, especially when small-scale disturbances such as windthrow, insect outbreaks (e.g., larch sawfly or eastern larch beetle) can create canopy gaps and uneven age structure, enhancing heterogeneity within and among stands (Bouchard and Pothier 2011).

In contrast, stagnant black spruce stands exhibited consistently lower structural complexity across multiple metrics. Persistent water-logged conditions constrain vertical growth, crown expansion, and regeneration, which limits recruitment of

shade-tolerant understory vegetation and results in relatively sparse understory layers. This creates structurally simpler stands that develop complexity more slowly over time. Overall, variation in structural metrics, such as variation in canopy cover, heterogeneity, and rumple, was more strongly associated with stand age alone, suggesting that structural variability increases over successional time, while being less influenced by broad cover type classification. This supports the idea that while categorical forest cover types capture some site-level differences, they may overlook finer-scale processes of structural development driven by succession, disturbance, and stand dynamics.

Importantly, our findings highlight how time and disturbance interact to shape structural heterogeneity. Within our study system, stand age largely reflects years post-harvest within a managed forest matrix, where timber harvest establishes initial stand conditions and resets structural development, while subsequent small-scale mortality, insect outbreaks, wind events, and hydrologic variability modify structure over time. Longer rotation lengths allow small-scale disturbances, including single-tree mortality, insect or disease events, and minor windthrow, to incrementally increase stand complexity (Anyomi et al. 2022). However, large-scale disturbances such as widespread eastern larch beetle outbreaks, severe blowdowns, or increasingly frequent fires driven by climate change and drought may overwhelm these benefits (Gough et al. 2022; McKee et al. 2022). Older peatland stands, especially those with higher structural complexity and accumulated downed wood, are also more vulnerable to drought stress and fire risk under changing climate conditions (Windmuller-Campione et al. 2024).

These dynamics underscore the importance of landscape-scale management strategies that consider both stand age and structural complexity. For example, applying a triad approach, combining intensively managed stands, reserves, and ecological forestry, can maintain diverse structural conditions across the landscape, balance economic and ecological values, and create young stands that can function as fuel breaks (Himes et al. 2022; Mast et al. 2025; D'Amato et al. 2025). Our study focused on relatively healthy stands without significant forest health concerns, but disturbances like eastern spruce dwarf mistletoe infection can create highly heterogeneous structural conditions within and among stands (Skay et al. 2021; Gray et al. 2025), further emphasizing the need to view peatlands through a landscape lens and to balance markets, disturbance risk, and long-term biodiversity goals (Mathiasen et al. 2008; Griebel et al. 2017). Together, these insights reinforce the ecological value of mature peatland stands as critical reservoirs of structural complexity and biodiversity, especially for species with narrow habitat requirements, and highlight the need to integrate age, disturbance, and fine-scale structure into management planning.

Overall bird metrics were stable across forest types and age classes, but peatland associate species showed clearer patterns, with significant increases in richness and diversity associated with stand age. Older peatland stands likely provide key structural features and resources that are particularly valuable to species with narrower habitat requirements (Imbeau et al. 2001; Laaksonen and Lehikoinen 2013). Consistent with this, lidar-derived metrics of canopy cover and overall complexity index were positively associated with peatland associate species richness and diversity, aligning with work demonstrating that structural heterogeneity promotes diverse

and abundant bird communities (MacArthur and MacArthur 1961; Müller et al. 2010; Goetz et al. 2010). Importantly, forest cover type was not a strong predictor of overall bird community metrics or peatland associate species, suggesting that broad vegetation classifications may not capture the fine-scale habitat features that influence avian diversity (Wiens 1989; Betts et al. 2003). This is an important result because forest cover and age are often the primary habitat characteristics available across large landscapes, and models such as WHINGS (Wildlife Habitat Indicator for Native Genera and Species; Zobel and Ek 2014) rely on these variables to predict habitat suitability. While this approach can be effective for predicting the presence of some generalist or widely distributed species, it may overlook the nuanced habitat requirements of specialists (Betts et al. 2006). In our study, stand age emerged as a more informative predictor, particularly for peatland associate species, which showed significant increases in richness and diversity with increasing age. This pattern likely reflects the development of structural features over time, such as snags and coarse woody debris that are critical habitat features used in nesting, foraging, and shelter (Imbeau et al. 2001, Peterson et al. 2023). Older stands likely provide expanded niche space through increased vertical layering and substrate diversity, allowing fine-scale resource partitioning among specialist species, consistent with classic niche theory and vertical foraging segregation described by MacArthur (1958) and subsequent work on habitat complexity and species coexistence (e.g., Tews et al. 2004). In addition, accumulated snags, coarse woody debris, and shrub development may supply important nesting and foraging substrates, while multi-layered canopies buffer microclimatic extremes. Together, these mechanisms suggest that structural complexity in peatland forests influences not only habitat form but also functional habitat availability. Because these features are not captured by cover type alone, and some may be only partially represented by lidar-derived canopy metrics, our results underscore the importance of multi-scale approaches that integrate lidar with detailed field-based measurements to more accurately characterize habitat complexity and its influence on biodiversity in peatland forests (Müller et al. 2010; Minayeva et al. 2017).

Ordination analyses further supported these patterns, revealing distinct bird communities in older, black spruce stands. This separation likely reflects underlying ecological differences: recent work by Sweeney et al. (2025) suggests that habitat complexity may shape not only which species occur where, but also the distribution of functional traits that influence ecosystem processes. Although formal functional diversity metrics in our study were limited by sample size and species richness, our community composition and Indicator Species Analysis provide indirect evidence of these functional patterns. For instance, species closely associated with mature black spruce stands, including Golden- and Ruby-crowned Kinglets, Boreal Chickadee, and Canada Jay, share traits such as reliance on dense conifer canopies for foraging, nesting, and food caching. These traits align with the structural attributes of older forests, highlighting how habitat complexity supports ecological functions linked to these specialized behaviors. In contrast, species found in less structurally complex, more open habitats included two peatland associate species (Lincoln's Sparrow and Palm Warbler) and several early-successional generalists (American Goldfinch, Savannah Sparrow, and Song Sparrow). Taken together, variation in habitat

complexity influences both species composition and functional traits, emphasizing the need to maintain landscape mosaics of open and structurally complex peatlands to support the full complement of specialist species and maximize gamma diversity, rather than assuming a single stand condition benefits all species.

Management Implications

Characterizing habitat complexity is central to understanding biodiversity patterns in boreal peatlands, where structural features strongly influence species distributions and ecological processes. Our results suggest that as stands mature, communities shift from more generalist-dominated assemblages toward more specialized peatland associate communities. This trajectory indicates that structural complexity expands functional niche space and supports species with narrower ecological requirements. Our findings also demonstrate the utility of lidar for quantifying canopy structure at landscape scales, while reinforcing the need for field-based measurements to capture structural elements not detectable remotely. Together, these results provide a mechanistic foundation for the use of ecological forestry to achieve structural complexity and the specialist species dependent on it in peatland forests.

Conventional, timber-centric management in peatland forests typically relies on clearcut harvesting at stem exclusion, which generally occurs between 60 and 100 years depending on site productivity (Windmuller-Campione et al. 2024). Stands are then allowed to regenerate naturally or are aerially seeded, with intermediate treatments uncommon due to economic constraints and reliance on winter-only access. This type of prescription aligns with the intensive, production-oriented approach in triad forest management (Himes et al. 2022) and may be suitable for maintenance of generalist species given their limited response to cover type and age class. However, strategic adjustments including extending rotation length and retaining structural legacies (live trees, snags, and coarse woody debris) during final harvest, could shift these treatments towards conditions more consistent with natural disturbance dynamics, aligning with the ecological forestry approach of triad forestry (Himes et al. 2022). By allowing greater accumulation of vertical layering and biological legacies, these adjustments would directly address the structural attributes associated with peatland associate species in our study and enhance habitat conditions for peatland associates and other specialist species (Koskela et al. 2007; Gustafsson et al. 2012).

Natural gap-based disturbance, arising from windthrow and biological disturbance agents especially eastern spruce dwarf mistletoe and historically eastern larch beetle, represents a natural structural template within these systems, providing a basis for ecological silviculture to achieve structural complexity (Windmuller-Campione et al. 2024). Silvicultural approaches that partially remove canopy cover, such as variable density thinning (Willis et al. 2018) or irregular shelterwood systems with reserves (Raymond et al. 2009), may approximate these dynamics by promoting spatial variability, vertical layering, and gap formation. Our findings suggest that time since structural reset is a fundamental driver of habitat development in peatland forests, with structural

attributes associated with specialist species emerging gradually as stands mature. Ecological forestry approaches that promote multi-cohort structure and size heterogeneity may function to compress this developmental timeline by introducing vertical layering and gap dynamics earlier in stand development, potentially increasing resilience under changing disturbance regimes. However, these practices are generally more complex and costly to implement and should be prioritized in areas where specialist species are most likely to benefit. Lastly, the ability to implement these practices may be increasingly constrained by climate change, as access has traditionally relied on frozen ground conditions that are becoming less predictable (Friesen et al. 2021). Nonetheless, managing for structural heterogeneity across cohorts and size classes may represent a central strategy for sustaining peatland biodiversity and ecosystem function under increasingly uncertain disturbance regimes.

Appendix

Tables 2 and 3

Table 2 Bird species classified as forested peatland associates, based on criteria from Green (1995), Niemi et al. (2016), and Pfannmuller et al. (2024)

Common name	Scientific name	Ecological niche
Black-backed Woodpecker	*Picoides arcticus*	Specializes in foraging on wood-boring beetle larvae within standing dead trees, often in older conifer stands
Blue-headed Vireo	*Vireo solitarius*	Nests and forages in mixed and coniferous forests, preferring dense understory and edge habitats
Boreal Chickadee	*Poecile hudsonicus*	Associated with mature black spruce and tamarack stands, gleaning insects from twigs and foliage
Canada Jay	*Perisoreus canadensis*	Inhabits spruce bogs and boreal forests, caching food for winter survival
Connecticut Warbler	*Oporornis agilis*	Favors dense, damp spruce and tamarack forests with thick understory layers
Dark-eyed Junco	*Junco hyemalis*	Common in northern forests; often nests on the ground in mossy or shrubby peatland areas
Golden-crowned Kinglet	*Regulus satrapa*	Inhabits mature conifer canopies, feeding on small arthropods among needles
Lincoln's Sparrow	*Melospiza lincolnii*	Associated with dense, moist shrub and wetland habitats, foraging low in vegetation for insects
Purple Finch	*Haemorhous purpureus*	Uses coniferous and mixed forests, foraging primarily on seeds and buds
Ruby-crowned Kinglet	*Regulus calendula*	Frequents dense spruce-fir and tamarack habitats, gleaning insects from foliage
Olive-sided Flycatcher	*Contopus cooperi*	Typically associated with open bogs and forest edges; hunts aerial insects from prominent perches
Palm Warbler	*Setophaga palmarum*	Nests in peatlands with open sphagnum and scattered stunted conifers; often forages near the ground
White-winged Crossbill	*Loxia leucoptera*	Specializes in extracting seeds from conifer cones, particularly in spruce-dominated stands
Yellow-bellied Flycatcher	*Empidonax flaviventris*	Breeds in mossy spruce and tamarack bogs; forages on insects near the forest floor
Yellow-rumped Warbler	*Setophaga coronata*	Generalist often associated with coniferous habitats; feeds on insects and berries across stand ages

These species occupy distinct ecological niches within forest peatland systems and collectively represent key components of peatland bird community composition

Table 3 Bird species recorded during two 10-min point count surveys (unlimited distance) conducted within each stand during the 2019 and 2020 breeding seasons

Common name	Scientific name	Alpha code
Alder Flycatcher	*Empidonax alnorum*	ALFL
American Goldfinch	*Spinus tristis*	AMGO
American Redstart	*Setophaga ruticilla*	AMRE
American Robin	*Turdus migratorius*	AMRO
Bay-breasted Warbler	*Setophaga castanea*	BBWA
Black-and-white Warbler	*Mniotilta varia*	BAWW
Black-backed Woodpecker*	*Picoides arcticus*	BBWO
Black-billed Magpie	*Pica hudsonia*	BBMA
Black-capped Chickadee	*Poecile atricapillus*	BCCH
Black-throated Green Warbler	*Setophaga virens*	BTNW
Blackburnian Warbler	*Setophaga fusca*	BLBW
Blue Jay	*Cyanocitta cristata*	BLJA
Blue-headed Vireo*	*Vireo solitarius*	BHVI
Boreal Chickadee*	*Poecile hudsonicus*	BOCH
Brown Creeper	*Certhia americana*	BRCR
Brown-headed Cowbird	*Molothrus ater*	BHCO
Canada Jay*	*Perisoreus canadensis*	CAJA
Cedar Waxwing	*Bombycilla cedrorum*	CEDW
Chestnut-sided Warbler	*Setophaga pensylvanica*	CSWA
Chipping Sparrow	*Spizella passerina*	CHSP
Common Raven	*Corvus corax*	CORA
Common Yellowthroat	*Geothlypis trichas*	COYE
Connecticut Warbler*	*Oporornis agilis*	CONW
Dark-eyed Junco*	*Junco hyemalis*	DEJU
Eastern Kingbird	*Tyrannus tyrannus*	EAKI
Eastern Wood-Pewee	*Contopus virens*	EAWP
Golden-crowned Kinglet*	*Regulus satrapa*	GCKI
Golden-winged Warbler	*Vermivora chrysoptera*	GWWA
Gray Catbird	*Dumetella carolinensis*	GRCA
Hairy Woodpecker	*Dryobates villosus*	HAWO
Hermit Thrush	*Catharus guttatus*	HETH
Least Flycatcher	*Empidonax minimus*	LEFL
Lincoln's Sparrow	*Melospiza lincolnii*	LISP
Magnolia Warbler	*Setophaga magnolia*	MAWA
Mourning Dove	*Zenaida macroura*	MODO
Mourning Warbler	*Geothlypis philadelphia*	MOWA
Nashville Warbler	*Leiothlypis ruficapilla*	NAWA
Northern Flicker	*Colaptes auratus*	NOFL
Northern Waterthrush	*Parkesia noveboracensis*	NOWA
Olive-sided Flycatcher*	*Contopus cooperi*	OSFL
Ovenbird	*Seiurus aurocapilla*	OVEN

Table 3 (continued)

Common name	Scientific name	Alpha code
Palm Warbler*	*Setophaga palmarum*	PAWA
Pine Siskin	*Spinus pinus*	PISI
Purple Finch*	*Haemorhous purpureus*	PUFI
Red Crossbill	*Loxia curvirostra*	RECR
Red-breasted Nuthatch	*Sitta canadensis*	RBNU
Red-eyed Vireo	*Vireo olivaceus*	REVI
Red-winged Blackbird	*Agelaius phoeniceus*	RWBL
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR
Ruby-crowned Kinglet*	*Regulus calendula*	RCKI
Savannah Sparrow	*Passerculus sandwichensis*	SAVS
Sedge Wren	*Cistothorus stellaris*	SEWR
Song Sparrow	*Melospiza melodia*	SOSP
Swamp Sparrow	*Melospiza georgiana*	SWSP
Tennessee Warbler	*Leiothlypis peregrina*	TEWA
Veery	*Catharus fuscescens*	VEER
White-throated Sparrow	*Zonotrichia albicollis*	WTSP
White-winged Crossbill*	*Loxia leucoptera*	WWCR
Wilson's Snipe	*Gallinago delicata*	WISN
Winter Wren	*Troglodytes hiemalis*	WIWR
Yellow Warbler	*Setophaga petechia*	YEWA
Yellow-bellied Flycatcher*	*Empidonax flaviventris*	YBFL
Yellow-rumped Warbler*	*Setophaga coronata*	YRWA

The table includes each species' common name, scientific name, and standardized four-letter alpha code. An asterisk (*) following the common name indicates a peatland habitat specialist

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Data Availability Data will be made available on request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

References

Aaseng, N. E., J. C. Almendinger, R. P. Dana, D. S. Hanson, M. D. Lee, E. R. Rowe, K. A. Rusterholz, and D. S. Wovcha. 2011. Minnesota's native plant community classification: A statewide classification of terrestrial and wetland vegetation based on numerical analysis of plot data. *Biological Report* 108:1–27.

Anderson, B. D., M. A. Windmuller-Campione, M. B. Russell, B. J. Palik, and D. N. Kastendick. 2020. Short- and long-term results of alternative silviculture in peatland black spruce in Minnesota, USA. *Forest Science* 66 (2): 256–265.

Anyomi, K. A., B. Neary, J. Chen, and S. J. Mayor. 2022. A critical review of successional dynamics in boreal forests of North America. *Environmental Reviews* 30 (4): 563–594.

Betts, M. G., S. E. Franklin, and R. G. Taylor. 2003. Interpretation of landscape pattern and habitat change for local indicator species using satellite imagery and geographic information system data in New Brunswick, Canada. *Canadian Journal of Forest Research* 33 (10): 1821–1831.

Bouchard, M., and D. Pothier. 2011. Long-term influence of fire and harvesting on boreal forest age structure and forest composition in eastern Québec. *Forest Ecology and Management* 261 (4): 811–820.

Boucher, J., C. Hébert, J. Ibarzabal, and É. Bauce. 2016. High conservation value forests for burn-associated saproxylic beetles: An approach for developing sustainable post-fire salvage logging in boreal forest. *Insect Conservation and Diversity* 9 (5): 402–415.

Bradford, J. B., and D. N. Kastendick. 2010. Age-related patterns of forest complexity and carbon storage in pine and aspen–birch ecosystems of northern Minnesota, USA. *Canadian Journal of Forest Research* 40 (3): 401–409.

Brassard, B. W., and H. Y. Chen. 2006. Stand structural dynamics of North American boreal forests. *Critical Reviews in Plant Sciences* 25 (2): 115–137.

Burns, R. M., and B. H. Honkala (technical coordinators). 1990. *Silvics of North America. Volume 1. Conifers; Vol. 2 Hardwoods.* Agriculture Handbook 654. USDA Forest Service, Washington, DC.

Carmean, W. H., J. T. Hahn, and R. D. Jacobs. 1989. *Site index curves for forest tree species in the eastern United States*. General Technical Report NC-128. USDA Forest Service North Central Forest Experiment Station, St. Paul, MN.

Cribari-Neto, F., and A. Zeileis. 2010. Beta regression in R. *Journal of Statistical Software* 34 (2): 1–24. https://doi.org/10.18637/jss.v034.i02.

Cyr, D., S. Gauthier, Y. Bergeron, and C. Carcaillet. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Frontiers in Ecology and the Environment* 7 (10): 519–524.

De Cáceres, M., and P. Legendre. 2009. Associations between species and groups of sites: Indices and statistical inference. *Ecology* 90 (12): 3566–3574. https://doi.org/10.1890/08-1823.1.

Dieleman, C. M., B. A. Branfireun, J. W. McLaughlin, and Z. Lindo. 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology* 21 (1): 388–395.

Dieleman, C. M., B. M. Rogers, S. Potter, S. Veraverbeke, J. F. Johnstone, J. Laflamme, K. Solvik, X. J. Walker, M. C. Mack, and M. R. Turetsky. 2020. Wildfire combustion and carbon stocks in the southern Canadian boreal forest: Implications for a warming world. *Global Change Biology* 26 (11): 6062–6079.

Dobson, A. P., A. D. Bradshaw, and A. J. Baker. 1997. Hopes for the future: Restoration ecology and conservation biology. *Science* 277 (5325): 515–522.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67 (3): 345–366.

Erwin, D. H. 2009. Climate as a driver of evolutionary change. *Current Biology* 19 (14): R575–R583.

Flannigan, M. D., M. A. Krawchuk, W. J. de Groot, B. M. Wotton, and L. M. Gowman. 2009. Implications of changing climate for global wildland fire. *International Journal of Wildland Fire* 18 (5): 483–507.

Fraixedas, S., A. Lindén, M. Piha, M. Cabeza, R. Gregory, and A. Lehikoinen. 2020. A state-of-the-art review on birds as indicators of biodiversity: Advances, challenges, and future directions. *Ecological Indicators* 118 : 106728.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, and K. Bible. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155 (1–3): 399–423.

Gauthier, S. 2009. *Ecosystem management in the boreal forest*. Quebec, Canada: Presses de l'Université du Québec.

Girona, M. M., Aakala, T., Aquilué, N., Bélisle, A. C., Chaste, E., Danneyrolles, V., Díaz-Yáñez, O., D'Orangeville, L., Grosbois, G., Hester, A., and Kim, S. 2023. Challenges for the sustainable management of the boreal forest under climate change. Boreal Forests in the face of climate change: sustainable management (pp. 773–837). Springer International Publishing.

Goetz, S. J., D. Steinberg, M. G. Betts, R. T. Holmes, P. J. Doran, R. Dubayah, and M. Hofton. 2010. Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. *Ecology* 91 (6): 1569–1576.

Gough, C. M., J. W. Atkins, R. T. Fahey, et al. 2022. Disturbance has variable effects on the structural complexity of a temperate forest landscape. *Ecological Indicators* 140 : 109004. https://doi.org/10.1016/j.ecolind.2022.109004.

Gray, E. R., M. B. Russell, and M. A. Windmuller-Campione. 2025. The role of eastern spruce dwarf mistletoe in stand dynamics of lowland black spruce forests in Minnesota, USA. *Canadian Journal of Forest Research* 55:1–10.

Green, J. C. 1995. *Birds and forests: A management and conservation guide*. St. Paul, MN: Minnesota Department of Natural Resources.

Griebel, A., D. Watson, and E. Pendall. 2017. Mistletoe, friend and foe: Synthesizing ecosystem implications of mistletoe infection. *Environmental Research Letters* 12 (11) : 115012.

Griffin, R. H. 1977. Direct seeding in northern forest types. P. 111–125 in *Gen. Tech. Rep. NE-29*. USDA Forest Service Northeastern Forest Experiment Station, Upper Darby, PA.

Grinde, A. R., R. Siebers, S. Kolbe, and J. Bednar. 2025. *Minnesota National Forest Breeding Bird Monitoring Program Annual Report: 1995–2025*. Technical Report NRRI/TR-2026/01. Natural Resources Research Institute, University of Minnesota Duluth.

Gustafsson, L., S. C. Baker, J. Bauhus, W. J. Beese, A. Brodie, J. Kouki, D. B. Lindenmayer, A. Lõhmus, G. M. Pastur, C. Messier, and M. Neyland. 2012. Retention forestry to maintain multifunctional forests: A world perspective. *BioScience* 62 (7): 633–645.

Hadley, A., and A. Desrochers. 2008. Winter habitat use by boreal chickadee flocks in a managed forest. *The Wilson Journal of Ornithology* 120 (1): 139–145.

Halme, P., K. A. Allen, A. Auniņš, R. H. Bradshaw, G. Brūmelis, V. Čada, J. L. Clear, A. M. Eriksson, G. Hannon, E. Hyvärinen, and S. Ikauniece. 2013. Challenges of ecological restoration: Lessons from forests in northern Europe. *Biological Conservation* 167:248–256.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3 (3): 329–382.

Himes, A., M. Betts, C. Messier, and R. Seymour. 2022. Perspectives: Thirty years of triad forestry, a critical clarification of theory and recommendations for implementation and testing. *Forest Ecology and Management* 510 : 120103.

Imbeau, L., M. Mönkkönen, and A. Desrochers. 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: A comparison with Fennoscandia. *Conservation Biology* 15 (4): 1151–1162.

IPCC. 2021. *Climate change 2021: The physical science basis*. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Masson-Delmotte, V. et al. (eds.). Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/9781009157896.

Kimmel, K., and Ü. Mander. 2010. Ecosystem services of peatlands: Implications for restoration. *Progress in Physical Geography* 34 (4): 491–514.

Koskela, E., M. Ollikainen, and T. Pukkala. 2007. Biodiversity conservation in commercial boreal forestry: The optimal rotation age and retention tree volume. *Forest Science* 53 (3): 443–452.

Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2012. Habitat complexity: Approaches and future directions. *Hydrobiologia* 685:1–17.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica* 36 (1): 97–125.

Kuuluvainen, T., and S. Gauthier. 2018. Young and old forest in the boreal: Critical stages of ecosystem dynamics and management under global change. *Forest Ecosystems* 5 (1): 1–15.

Laaksonen, T., and A. Lehikoinen. 2013. Population trends in boreal birds: Continuing declines in agricultural, northern, and long-distance migrant species. *Biological Conservation* 168:99–107.

Lefsky, M. A., W. B. Cohen, G. G. Parker, and D. J. Harding. 2002. Lidar remote sensing for ecosystem studies. *BioScience* 52 (1): 19–30.

Lindenmayer, D. B., C. R. Margules, and D. B. Botkin. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* 14 (4): 941–950.

Lindenmayer, D. B., and J. F. Franklin. 2013. *Conserving forest biodiversity: A comprehensive multiscaled approach*. Washington, DC: Island Press.

Liu, X., Y. Feng, T. Hu, Y. Luo, X. Zhao, J. Wu, E. E. Maeda, W. Ju, L. Liu, Q. Guo, and Y. Su. 2024. Enhancing ecosystem productivity and stability with increasing canopy structural complexity in global forests. *Science Advances* 10 (20) : eadl1947.

Lunde, L. F., T. Birkemoe, A. Sverdrup-Thygeson, J. Asplund, R. Halvorsen, O. J. Kjønaas, J. Nordén, S. Maurice, I. Skrede, L. Nybakken, and H. Kauserud. 2025. Towards repeated clear-cutting of boreal forests—A tipping point for biodiversity? *Biological Reviews* 100 (3): 1181–1205.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39 (4): 599–619.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42 (3): 594–598.

Majasalmi, T., and M. Rautiainen. 2020. The impact of tree canopy structure on understory variation in a boreal forest. *Forest Ecology and Management* 466 : 118100.

Mast, C. N., N. G. Williams, M. G. Betts, and M. S. Lucash. 2025. Land sharing, land sparing, and Triad forestry: Modeling forest composition, diversity, and carbon storage under climate change and natural disturbances. *Landscape Ecology* 40 (2): 1–22.

Mathiasen, R. L., D. L. Nickrent, D. C. Shaw, and D. M. Watson. 2008. Mistletoes: Pathology, systematics, ecology, and management. *Plant Disease* 92 (7): 988–1006.

McElhinny, C., P. Gibbons, C. Brack, and J. Bauhus. 2005. Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management* 218 (1–3): 1–24.

McFarlane, K. J., P. J. Hanson, C. M. Iversen, J. R. Phillips, and D. J. Brice. 2018. Local spatial heterogeneity of Holocene carbon accumulation throughout the peat profile of an ombrotrophic Northern Minnesota bog. *Radiocarbon* 60 (3): 941–962.

McGaughey, R. J. 2016. *FUSION/LDV: Software for LiDAR data analysis and visualization—V3. 10*. Washington, DC: USDA Forest Service.

McKee, F. R., M. A. Windmuller-Campione, E. R. Althoff, M. R. Reinikainen, P. A. Dubuque, and B. H. Aukema. 2022. Chapter 9 - Eastern larch beetle, a changing climate, and impacts to northern tamarack forests. In Bark Beetle Management, Ecology, and Climate Change. Edited by Gandhi, K.J.K., Hofstetter, R.W. Academic Press; 2022:261-300.

Minnesota Geospatial Information Office (MnGeo). 2025. *Minnesota Geospatial Commons geospatial datasets (lidar)*. Minnesota IT Services, St. Paul, MN, USA. Available at: https://gisdata.mn.gov/lt/dataset/elev-lidar-statewide-gen2. Accessed 10 Apr 2025.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 (6772): 853–858.

Niemi, G., J. Hanowski, P. Helle, R. Howe, M. Mönkkönen, L. Venier, and D. Welsh. 1998. Ecological sustainability of birds in boreal forests. *Conservation Ecology* 2 (2): 17.

Niemi, G.J ., R. W. Howe, B. R. Sturtevant, L. R. Parker, A. R. Grinde, N. P. Danz, M. D. Nelson, S. M. Lietz, and E. L. Lindquist. 2016. *Analysis of long-term forest bird monitoring data from national forests of the western Great Lakes region*. General Technical Report NRS-159. USDA Forest Service Northern Research Station, Newtown Square, PA.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2025. *vegan: Community Ecology Package*. R package version 2.6-6. https://doi.org/10.32614/CRAN.package.vegan.

Page, S. E., and A. J. Baird. 2016. Peatlands and global change: Response and resilience. *Annual Review of Environment and Resources* 41 (1): 35–57.

Parish, F., A. A. Sirin, D. Charman, H. Joosten, T. Y. Minaeva, and M. Silvius (eds.). 2008. *Assessment on peatlands, biodiversity and climate change*. Global Environment Centre, Kuala Lumpur and Wetlands International, Kuala Lumpur, Malaysia.

Peterson, D. W., E. K. Dodson, and R. J. Harrod. 2023. Snag decomposition following stand-replacing wildfires alters wildlife habitat use and surface woody fuels through time. *Ecosphere* 14 (8) : e4635.

Pfannmuller, L. A., G. J. Niemi, and J. C. Green. 2024. *The breeding birds of Minnesota: History, ecology, and conservation*. University of Minnesota Press, Minneapolis, MN, USA.

Puettmann, K. J., A. W. D'Amato, U. Kohnle, and J. Bauhus. 2009. Individual-tree growth dynamics of mature *Abies alba* during repeated irregular group shelterwood (Femelschlag) cuttings. *Canadian Journal of Forest Research* 39 (12): 2437–2449.

R Core Team. 2025. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 16 May 2025

Raymond, P., S. Bédard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. *Journal of Forestry* 107 (8): 405–413.

Raymond, P., M. Löf, P. Comeau, L. Rytter, M. M. Girona, and K. J. Puettmann. 2023. In *Boreal forests in the face of climate change: Sustainable management*, ed. M.M Girona, M.H. Morin, S. Gauthier, and Y. Bergeron, 403-416. Berlin: Springer International Publishing, Cham, Switzerland.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. *Science* 366 (6461): 120–124.

Rydin, H., J. K. Jeglum, and K. D. Bennett. 2013. *The biology of peatlands*. 2nd ed. Oxford University Press, Oxford, UK.

Skay, R., M. A. Windmuller-Campione, M. B. Russell, and L. F. Reuling. 2021. Influence of eastern spruce dwarf mistletoe on stand structure and composition in northern Minnesota. *Forest Ecology and Management* 481 : 118712.

Soja, A. J., N. M. Tchebakova, N. H. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin III., and P. W. Stackhouse Jr. 2007. Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* 56 (3–4): 274–296.

Stelling, J. M., R. A. Slesak, M. A. Windmuller-Campione, and A. R. Grinde. 2023. Effects of stand age, tree species, and climate on water table fluctuations and estimated evapotranspiration in managed peatland forests. *Journal of Environmental Management* 339 : 117783.

Sweeney, C. P., W. Peterman, K. Zhao, K. Goodell, B. Zuckerberg, and M. A. Jarzyna. 2025. Three-dimensional habitat structure drives avian functional and trait diversity across North America. *Ecology and Evolution* 15 : e70988. https://doi.org/10.1002/ece3.70988.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography* 31 (1): 79–92.

Thompson, I. D., D. J. Larson, and W. A. Montevecchi. 2003. Characterization of old "wet boreal" forests, with an example from balsam fir forests of western Newfoundland. *Environmental Reviews* 11 (S1): S23–S46.

Thompson, P. L., B. Rayfield, and A. Gonzalez. 2017. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography* 40 (1): 98–108.

Venier, L. A., and J. L. Pearce. 2004. Birds as indicators of sustainable forest management. *Forestry Chronicle* 80 (1): 61–66.

Viereck, L. A., and W. F. Johnston. 1990. In: Burns, R. M. and B. H. Honkala (tech coords.), Silvic of North America, Vol. 1. Conifers. USDA Forest Service Handbook 654, Washington, DC, USA.

Wagner, C. V. 1978. Age-class distribution and the forest fire cycle. *Canadian Journal of Forest Research* 8 (2): 220–227.

Wells, J. V., and P. J. Blancher. 2011. Global role for sustaining bird populations. *Studies in Avian Biology* 41:7–22.

Wiens, J. A. 1989. *The ecology of bird communities: Volume 1, Foundations and patterns.* Cambridge University Press, Cambridge, UK.

Willis, J. L., S. D. Roberts, and C. A. Harrington. 2018. Variable density thinning promotes variable structural responses 14 years after treatment in the Pacific Northwest. *Forest Ecology and Management* 410:114–125.

Windmuller-Campione, M. A., M. B. Russell, E. Sagor, A. W. D'Amato, A. R. Ek, K. J. Puettmann, and M. G. Rodman. 2020. The decline of the clearcut: 26 years of change in silvicultural practices and implications in Minnesota. *Journal of Forestry* 118 (3): 244–259.

Windmuller-Campione, M. A., L. F. Reuling, R. A. Slesak, and R. K. Kolka. 2024. Ecological silviculture for lowland wet conifer forest lake states. In *Ecological Silvicultural Systems: Exemplary Models for Sustainable Forest Management.* Edited by B.J. Palik and A.W. D'Amato. John Wiley & Sons, Ltd. Hoboken, NJ. pp. 81-97

Wing, B. M., M. W. Ritchie, K. Boston, W. B. Cohen, A. Gitelman, and M. J. Olsen. 2012. Prediction of understory vegetation cover with airborne lidar in an interior ponderosa pine forest. *Remote Sensing of Environment* 124:730–741.

Wright, H. E., B.A. Coffin, and N. E. Aaseng (eds). 1992. *The patterned peatlands of Minnesota*. University of Minnesota Press, Minneapolis, MN, USA.

Zobel, J.M., and A.R. Ek. 2014. *The Wildlife Habitat Indicator for Native Genera and Species (WHINGS): Methodology and application*. Staff Paper Series 231. Department of Forest Resources, University of Minnesota, St. Paul, MN.

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